

Micronuclei averaged 1.43 per pollen mother cell. The hybrid is completely sterile.

Although it was not possible to distinguish between autosyndetic and allosyndetic pairing, the high frequency of quadrivalents in the hybrid suggests that important homologies exist between the parental species.

The hybrid is morphologically intermediate between the two parents except for size relationships. Some support is given to the suggestion that *Agropyron saundersii* had a similar origin.

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CYTOTAXONOMIC OBSERVATIONS ON *MENTZELIA*, SECT. *BARTONIA* (LOASACEAE)

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A previous investigation (Thompson & Lewis, 1955) stated that information about chromosome numbers in *Mentzelia* would be of great value in the formation of evolutionary and taxonomic concepts in the genus. Section *Trachyphytum*, represented by twenty populations of ten species, was shown to be a polyploid complex on the base $x=9$, with diploids ($n=9$), tetraploids ($n=18$), hexaploids ($n=27$), and octaploids ($n=36$). On the other hand, polyploids were not found in section *Bartonia*, although only two species were examined cytologically: *Mentzelia multi-*

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flora with $n=9$ and *M. laevicaulis* with $n=11$. The present paper reports chromosome numbers of $n=9$, 10, and 11, from forty-eight populations representing eleven of the approximately twenty species of section *Bartonia*, and establishes that aneuploidy, rather than polyploidy, is a major feature of evolution in this section.

Section *Bartonia* is clearly distinct from all other sections of *Mentzelia*. In section *Bartonia* the seeds are flat and circular in outline, with the margin extended into a wing. The flowers are relatively large and the five petals grade into the stamens through petaloid staminodia or at least broad-filament stamens. The plants are rosette-perennials and flower in late spring or summer. The flowers open and shed pollen in the late afternoon or evening and are pollinated by bees or hawk moths. Most of the species occur in the Rocky Mountain area of the United States, but one, *M. albescens*, also occurs in Argentina and Chile. This delimitation of section *Bartonia* agrees with that of Urban and Gilg (1900) and also with the description of the section by Darlington (1934). Darlington, however, without discussion included *M. torreyi* and *M. reflexa* in section *Bartonia*, perhaps inadvertently, because she did not modify her description of the section to accommodate them. They are clearly more similar to species of other sections.

CHROMOSOME NUMBERS IN BARTONIA

The nomenclature under which the following chromosome numbers are reported largely follows the most recent monograph of the genus (Darlington, 1934). The characteristics of the species as understood in this study are given briefly so that the chromosome numbers are clearly associated with groups of natural populations. All observations of chromosomes were made in squashed microsporocytes, using procedures previously described (Thompson, 1960). Voucher specimens are on file in the herbarium of the University of California, Los Angeles (LA).

MENTZELIA LAEVICAULIS (Dougl. ex Hook.) Torr. & Gray $n=11$

Thompson 3089, 3197, 5 miles northwest of Gardiner, Park County, Montana.

" 1690, 35 miles northeast of Garrison, Millard County, Utah.

" 3195, 42 miles southwest of Ely, Nye County, Nevada.

" 3194, Montgomery Pass, Mineral County, Nevada.

Mentzelia laevicaulis is widespread west of the Rocky Mountains, crossing that range into Montana and Wyoming. It is very distinct, with flowers that have five yellow petals 4–6 cm. long. There are no staminodia, but the five outer stamens have slightly broadened filaments about 2 mm. wide. The bracts at the base of the capsule are linear-lanceolate and entire or with up to four short, pinnate lobes. Over one hundred individuals from ten widely scattered populations (see also Thompson & Lewis, 1955) have been examined cytologically and all had eleven pairs of chromosomes with two of the pairs conspicuously larger than the other nine.

MENTZELIA DECAPETALA (Pursh) Urban & Gilg $n=11$

- Thompson* 3198, 5 miles northwest of Gardiner, Park County, Montana.
 " 3206, 1 mile northwest of Florence, Fremont County, Colorado.
Ernst 746, east of Hennessey, Kingfisher County, Oklahoma.
Thompson 3098, 5 miles south of Raton, Colfax County, New Mexico.
 " 2084, 25 miles southeast of Lubbock, Crosby County, Texas.

Mentzelia decapetala is widespread east of the Rocky Mountains from Idaho and Alberta south to Texas. In habit the plants are much like *M. laevicaulis*, but the flowers have ten white petals (five petals and five staminodia) 5–8 cm. long. The bracts are pectinate and borne on the sides of the capsule. None of the chromosomes of *M. decapetala* is as large as the two largest chromosomes in the *M. laevicaulis* genome. The chromosome number of *M. decapetala* was reported as $n=11$ by Hamel (1938), but no voucher specimen was cited. *Mentzelia decapetala* and *M. laevicaulis* hybridize readily where they grow together near Gardiner, Montana (*Thompson* 3086, 3087, and 3199). The hybrids are common, easily recognized, produce very little good pollen, and set no viable seeds.

MENTZELIA NUDA (Pursh) Torr. & Gray $n=10$

- Thompson* 1800, 2 miles north of Big Springs, Deuel County, Nebraska.
 " 3097, 15 miles south of Fountain, Pueblo County, Colorado.
 " 1676, 6 miles east of Walsenberg, Huerfano County, Colorado.
 " 2085, 25 miles southeast of Lubbock, Crosby County, Texas.

Mentzelia nuda occurs on the plains east of the Rocky Mountains from Montana to Texas. The plants are 5–10 dm. tall, with the older plants producing five or six strict stems from the caudex. The pubescence is dense and the leaves are the most scabrous in the section. The white petals and petaloid staminodia, about ten in number, grade into the stamens through numerous narrow staminodia. The bracts at the base of the capsule are lacinate.

The identity of *M. nuda* has been a matter of some confusion. Pursh (1814, p. 328) based his description on plants grown from seed gathered by Nuttall in 1811 along the Great Bend of the Missouri River. According to Pennell (1936, p. 14) this locality is between the White River and the present city of Pierre, South Dakota. Pursh (*loc. cit.*) says, "This species has smaller flowers, and the leaves are not so glaucous as the foregoing [*M. decapetala*]; in every other respect the above description is applicable to the present one . . .". Considering these remarks and the locality, the name can apply only to the species considered here. I consider *M. stricta* (Osterh.) Stevens ex Jeffs and Little a synonym. The Nuttall specimen cited by Darlington (1934, p. 163) is not the type of *M. nuda*; Pursh apparently never saw it. Most plants cited by Darlington (1934, p. 162–3) as *M. nuda* are referable to *M. multiflora*.

MENTZELIA STRICTISSIMA (Woot. & Standl.) Darl. $n=10$

- Thompson* 2081, 4 miles west of Fort Sumner, De Baca County, New Mexico.
 " 2087, 26 miles southwest of Odessa, Ector County, Texas.

This species occurs in eastern New Mexico and western Texas, partic-

ularly in the drainage of the Pecos River. It is most similar to *M. nuda*, differing only in its smaller flowers (petals less than 25 mm. long) and more entire bracts. *Mentzelia strictissima* is not known to occur sympatrically with *M. nuda*, and these two taxa may be only geographical races.

MENTZELIA RUSBYI Woot. n=10

Thompson 1670, 2 miles north of Eagle Nest, Colfax County, New Mexico.

" *3103*, 18 miles southwest of Las Vegas, San Miguel County, New Mexico.

" *1665*, 6 miles east of Flagstaff, Coconino County, Arizona.

The plants of the collections cited here are erect, not branched below, and the inflorescence is compact. The rosette leaves are linear, about 15 cm. long, 8 mm. wide, and dentate to nearly entire. The petals are 15–20 mm. long, white and often with a tinge of apricot at the apex. The bracts at the base of the capsule are pinnately lobed. Harrington (1954) has considered *M. rusbyi* and *M. nuda* to be only varietally distinct [*M. nuda* (Pursh) Torr. & Gray var. *rusbyi* (Woot.) Harr.].

MENTZELIA CHRYSANTHA Engelm. n=10

Thompson 3096, 1 mile north of Florence, Fremont County, Colorado.

Mentzelia chrysantha was described from plants collected near Canyon City, Colorado, from the same vicinity as the collection cited here. The plants of this species have numerous lower branches, which are decumbent, and a compact inflorescence. The petals are golden-yellow and the leaves are lanceolate and shallowly lobed. The bracts at the base of the cylindrical capsules are entire and the seeds are narrowly winged.

MENTZELIA SPECIOSA Osterh. n=10

Thompson 3093, 5 miles south of Castle Rock, Douglas County, Colorado.

The collection here referred to *M. speciosa* fits the original description very well. The petals are golden-yellow, much like those of *M. chrysantha*, but the inflorescence is open, the stems reddish, not white, the leaves more deeply lobed, the seeds more broadly winged, and the lower branches are fewer and not decumbent. The name *M. speciosa* has not been used since Darlington (1934) placed it in synonymy under *M. multiflora* (Nutt.) Gray; however, the type of *M. multiflora* is from Santa Fe, New Mexico, and has straw-white petals. Furthermore, recent collections from the Santa Fe area that match the type of *M. multiflora* have nine pairs of chromosomes. *Mentzelia speciosa* is apparently restricted to the east slope of the Rocky Mountains of Colorado.

MENTZELIA Densa Greene n=10

Thompson 1684, Cotopaxi, Arkansas River, Fremont County, Colorado.

The plants of the population studied are 3–4 dm. tall with many branches from the caudex. The petals are golden-yellow, 16–18 mm. long, and grade through staminodia into the stamens. The capsules are cylindrical, tapered at the base, 10–13 mm. long, and subtended by a linear, entire bract. The leaves are 4–8 cm. long, pinnate, usually with six lobes,

these 4 mm. long and 2 mm. wide, with the midrib 2 mm. wide. These plants agree very well with Greene's (1896) original description. Darlington (1934) cited only three specimens under *M. densa*, all from the Grand Junction area of western Colorado, although Greene (1896) stated, "Common in the Cañon of the Arkansas in southern Colorado, and elsewhere among the foothills".

MENTZELIA LACINIATA (Rydb.) Darl. n=10

Thompson 1687, 11 miles west of Pagosa Springs, Archuleta County, Colorado.

The plants of this population have golden-yellow petals and are generally similar to *M. densa* but differ in having more deeply lobed, lacinate leaves and narrowly winged seeds. *Mentzelia laciniata* has been reported from southwestern Colorado and northwestern New Mexico.

MENTZELIA MULTIFLORA (Nutt.) Gray n=9

Thompson 3095, 7 miles north of Penrose, Fremont County, Colorado.

- " 1675, 3 miles west of La Veta Pass Summit, Costilla County, Colo.
- " 3099, 8 miles south of Raton, Colfax County, New Mexico.
- " 3100, 18 miles southwest of Las Vegas, San Miguel County, New Mexico.
- " 1672, 6 miles west of Red River, Taos County, New Mexico.
- " 1669, 7 miles east of Taos, Taos County, New Mexico.
- " 1668, 25 miles southwest of Taos, Taos County, New Mexico.
- " 1667, 38 miles west of Albuquerque, Bernalillo County, New Mexico.
- " 2076, 15 miles northwest of Datil, Catron County, New Mexico.
- " 2074, 4 miles east of Quemado, Catron County, New Mexico.
- " 3107, 6 miles east of Pie Town, Catron County, New Mexico.
- " 2091, 5 miles west of Las Cruces, Doña Ana County, New Mexico.
- " 2089, 6 miles east of Allamore, Hudspeth County, Texas.
- " 2088, 7 miles east of Pecos, Ward County, Texas.
- " 3212, 1 mile west of Sanders, Apache County, Arizona.
- " 1666, Highway 66 at Painted Desert, Apache County, Arizona.
- " 3222, 3 miles west of Winkelman, Pinal County, Arizona.
- " 2094, 21 miles northeast of Benson, Cochise County, Arizona.
- " 1664, 10 miles southwest of Prescott, Yavapai County, Arizona.
- " 1662, 2 miles northeast of Congress Jct., Yavapai County, Arizona.
- " 2067, Salt River at Highway 60, Gila County, Arizona.
- " 2066, 10 miles west of Globe, Gila County, Arizona.

Raven 14818, 13 miles north of Puerto Peñasco, Sonora, Mexico.

Plants of the kind referred here occur in most of the western states and in northern Mexico and, as delimited in Darlington's monograph (1934), they form the most variable complex in the section. All the plants in this group have petals 15–25 mm. long, yellow to nearly white, that grade through broad staminodia into the stamens. The capsules are cylindrical to urceolate, 15–25 mm. long, usually with a linear, entire bract at the base and with seeds that are broadly winged. The leaves are pinnately lobed to dentate. *Mentzelia multiflora* (Nutt.) Gray obviously applies to this group of plants. The type was collected by Gambel near Santa Fe, New Mexico, and was described as having petals $\frac{3}{4}$ inch long, straw-white in color. My collections from this region in New Mexico that agree with the original description have nine pairs of chromosomes. *Mentzelia*

nuda (Pursh) Torr. & Gray is sometimes incorrectly applied to this group of plants.

Four of the collections cited here, *Thompson 1664, 1662, 2067, and 2066*, differ from the others in having the darkest yellow petals, the most urceolate capsules, and more entire leaves. Plants of this kind grow in the mountains of central Arizona between the southern desert and the Mogolon Rim.

MENZELIA MULTICAULIS (Osterh.) Darl. $n=11$

Thompson 3201, Dinosaur National Monument, Uinta County, Utah.

" 3203, 8 miles west of Rio Blanco, Rio Blanco County, Colorado.

" 3205, 1 mile north of Walcott, Eagle County, Colorado.

Mentzelia multicaulis occurs in northwestern Colorado and northeastern Utah. The flowers have five yellow petals, but the next inner whorl may be either five staminodia or five stamens with filaments nearly as broad as the petals. A distinctive characteristic of *M. multicaulis* is that either the petals, the staminodia, or both are very broad, 9 mm. long and 6 mm. wide. In this species the capsules are urceolate, 8 mm. long and subtended by a linear bract. The seeds have very narrow wings. The lower leaves are 4–6 cm. long, pinnatifid, the four to six lobes are nearly 1 cm. long and 2 mm. wide and the midrib is 3 mm. wide. The upper leaves are entire and linear. All of the plants observed were more than one year old and had several stems 1–3 dm. long from the old caudex. *Mentzelia multicaulis* is most similar to *M. humilis* (Gray) Darl., but the latter differs in having the petals and staminodia short and narrow and seeds with broad wings.

Chromosome numbers have been reported for two other species of section *Bartonia*. *Mentzelia albescens* (Gill.) Griseb., the only species of section *Bartonia* in South America, was reported as $n=11$ by Covas and Schnack (1946) from material collected at Luján, Provincia de Mendoza, Argentina. Hamel (1938) reported $n=9$ from root-tip sections of plants identified by him as *M. humilis*. Hamel did not cite a voucher specimen and the identity of his material is unknown. The seeds for his culture were obtained from the New York Botanical Garden.

SUMMARY AND CONCLUSION

Two sections of *Mentzelia*, sections *Bartonia* and *Trachyphytum*, are morphologically more similar to each other than to any of the other sections. However, their validity as distinct phylads within the genus is indicated not only by consistent morphological differences but also by contrasting patterns of chromosomal change in the course of their evolution. Section *Trachyphytum* has only one basic chromosome number ($x=9$) although it comprises diploid, tetraploid, hexaploid, and octaploid species that form one large polyploid complex. Section *Bartonia*, on the other hand, has no known polyploid species, but three basic chromosome numbers are present in the group; one highly variable species has $n=9$, seven

species have $n=10$, and four species have $n=11$. The prevalence of polyploidy in one section and aneuploidy in the other undoubtedly reflects a fundamental difference in genetic systems and a corresponding phylogenetic separation of the two sections.

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A REVISION OF THE GENUS *THAXTEROGASTER* SINGER

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Since the original publication of the genus *Thaxterogaster* (Singer, 1951) and the subsequent monograph (Singer & Smith, 1958), further studies have been made as time and available material permitted, and these have led to the discovery of additional species. Species are here grouped into sections, since certain distinct trends are now evident. Those species treated in detail in our monograph (*loc. cit.*) are not redescribed here, but detailed accounts of new or transferred taxa are treated critically.

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¹ Papers from the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Buenos Aires, Argentina, and the University Herbarium and Department of Botany (Paper no. 1142), the University of Michigan, Ann Arbor, Michigan, U.S.A.